



SMALL MAMMALS FROM SERRA DO BRIGADEIRO STATE PARK,
MINAS GERAIS, SOUTHEASTERN BRAZIL:
SPECIES COMPOSITION AND ELEVATIONAL DISTRIBUTION ¹

(With 5 figures)

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ABSTRACT: The Serra do Brigadeiro State Park represents one of the few remnants of Atlantic forest in a mountainous region of the State of Minas Gerais. The terrestrial small mammal fauna of the park within a 1200-1800m altitudinal interval was inventoried from 1996 to 2004 to generate estimates about taxonomic composition, richness, abundance, and altitudinal distribution of species. Cytogenetic analyses were carried out for selected species as an additional tool for taxonomic identifications and diversity estimates. A sampling effort of 4620 trapping-nights resulted in 21 species of rodents (families Cricetidae and Echimyidae) and marsupials (family Didelphidae) recorded, of which seven have their karyotypes described. Cumulative curves and non-parametric estimators suggest that the overall inventory is 81% complete and that at least five species are likely to be recorded with additional sampling. Species composition and diversity varied significantly across elevational belts with the lower altitudes characterized by both forest restricted and habitat-generalist species, while the upper altitudes are exclusively characterized by elevationally widespread and habitat-generalist species. Species diversity peaked at middle elevations (1300-1400m) and the putative factors responsible for this pattern are discussed.

Key words: Altitudinal variation. Serra do Brigadeiro. Estimates. Species richness. Campos de altitude.

RESUMO: Pequenos mamíferos do Parque Estadual da Serra do Brigadeiro, Minas Gerais, Sudeste do Brasil: composição de espécies e distribuição altitudinal.

O Parque Estadual da Serra do Brigadeiro é um dos poucos remanescentes de Mata Atlântica, na Zona da Mata de Minas Gerais, localizado em região montanhosa. No período entre 1996 e 2004, foi empreendido um esforço de captura de 4620 armadilhas-noite, amostrando o intervalo altitudinal 1200-1800m, com o objetivo de inventariar a fauna de pequenos mamíferos terrestres, produzir estimativas sobre a composição taxonômica, riqueza, abundância e distribuição altitudinal das espécies desse grupo no parque. Análises citogenéticas foram realizadas em algumas espécies para auxiliar a identificação taxonômica. Foram registradas 21 espécies de roedores e marsupiais (famílias Cricetidae, Echimyidae e Didelphidae), sete das quais tiveram seus cariótipos descritos. O padrão de diversidade revelado pelas curvas cumulativas de espécie e estimadores não-paramétricos sugere que aproximadamente 81% da riqueza de espécies foi amostrada e que pelo menos cinco espécies possam ser adicionadas à listagem com esforço de captura adicional. A riqueza e composição de espécies variaram significativamente entre as cotas altimétricas, sendo as áreas mais baixas caracterizadas pela presença simultânea de espécies restritas à mata e espécies generalistas, enquanto a comunidade das áreas mais elevadas foi composta exclusivamente por

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espécies com ampla distribuição altitudinal e generalistas com relação ao hábitat. A maior riqueza de espécies foi detectada nas altitudes intermediárias (1300-1400m), sendo discutidos os fatores possivelmente responsáveis por esse padrão.

Palavras-chave: Variação altitudinal. Serra do Brigadeiro. Estimativas. Riqueza de espécies. Campos de altitude.

INTRODUCTION

The Atlantic Forest Morphoclimatic Domain that once extended from the coast of Northeastern Brazil southward to Paraguay, Argentina, and Southern Brazil has approximately 95% of its original cover replaced by human environments (ARAÚJO, 2000; TABARELLI *et al.*, 2005). This severe habitat loss, allied to the presence of an exceptional number of endemic species of vascular plants and vertebrates, ranked the Atlantic forest among the five top priority areas for conservation in the world (MYERS *et al.*, 2000). Nevertheless, conservation strategies concerning this domain largely depend on basic knowledge about the geographic distribution of species, endemism levels, and local diversity. Unfortunately, such knowledge is still lacking for many Atlantic forest remnants in eastern Brazil, even concerning well studied taxa such as mammals.

The Southeastern region of the Atlantic forest presents a complex topography, being traversed by two major mountain complexes, the Serra do Mar and Serra da Mantiqueira (COSTA *et al.*, 2000), which encompass a broad altitudinal interval (0-2900m) and a considerable variation in climates and vegetation. Early mammal surveys in the Atlantic forest were already directed to these montane areas (MIRANDA-RIBEIRO, 1905, 1935; DAVIS, 1945), but few inventories extended their sampling efforts to the higher altitudinal zones. The more recent attempts conducted in two major mountain ranges of southeastern Brazil (the Itatiaia and Caparaó massifs) have revealed the occurrence of a number of altitudinally restricted endemic species of cricetid rodents (*e.g.*, *Akodon mystax*, *Oxymycterus caparae*), generally overlooked by past inventory efforts (BONVICINO *et al.*, 1997; HERSHKOVITZ, 1998; GEISE *et al.*, 2004). Despite these initial efforts, the patterns of altitudinal variation in species diversity and abundance are still poorly known for non-volant small mammals in Atlantic forest.

A global biogeographic pattern observed for non-volant small mammals in montane systems has been the mid-domain effect, in which species diversity tends to peak at middle altitudes. The causes of the mid-domain pattern have been recurrently debated in discussions of montane

biogeography (LOMOLINO, 2001; MCCAIN, 2004; COLWELL *et al.*, 2004), but the generality of this pattern has been rarely tested in Atlantic forest montane communities due to the paucity of local inventories across altitudinal gradients.

The Serra do Brigadeiro State Park represents one of the few remnants of Atlantic forest in a mountainous region of the State of Minas Gerais. The first inventories in the area (MOOJEN, 1937) reported a remarkable set of large mammals, including the northern muriqui (*Brachyteles hypoxanthus*), the jaguar (*Panthera onca*) and the giant otter (*Pteronura brasiliensis*). The steady threaten of these large sized mammals in the Atlantic forest led to the indication of the Serra do Brigadeiro as a priority area for conservation and wildlife research (COSENZA & MELO, 1998; CONSERVATION INTERNATIONAL OF BRAZIL, 2000). Despite this relevance, the diverse small-bodied mammals of the area remained sparsely studied on subsequent publications about the fauna of the Serra do Brigadeiro.

In this paper, we report the results of a small terrestrial mammal inventory conducted at three localities within the park. We first provide a list of the marsupials and small rodents recorded, complementing taxonomic identifications of some species with cytogenetic data. Second, we describe the altitudinal distribution of species richness, abundance, and taxonomic composition. The performance of the inventory is evaluated through cumulative curves and non-parametric richness estimators.

MATERIAL AND METHODS

STUDY AREA

The Serra do Brigadeiro is an eastern offshoot of the Serra da Mantiqueira extending to the eastern part of the State of Minas Gerais in southeastern Brazil (Fig.1; longitudes 42°40' to 40°20'W and latitudes 20°33' to 21°00'S). The park encompasses an area of 13,210 hectares, including most of the Serra do Brigadeiro with elevations varying from 1000 up to 1890m, at the Pico do Soares, the highest mountaintop in the region (LEONI & TINTE, 2004; FONTES *et al.*, 2003). The mean rainfall varies from

1000 to 2000 millimeters throughout the year, a regime typical of a seasonal humid climate (Cwb of Köppen system) with two well defined seasons: the rainy (October to March) and the dry (April to September) (LEONI & TINTE, 2004; FONTES *et al.*, 2003). The area is included in the phytoecological region of Semideciduous Atlantic Forest (IBGE, 2004) but three distinct phytophysognomies can be identified: 1) submontane forest – covers the mountain slopes and represents the predominant vegetational type in the park; there are three well defined arboreal strata in more mature forests: lower (4 to 15m), medium (15 to 20m), and upper (higher than 20m); 2) transitional areas – these areas are intermediate between the submontane forests and mountaintop grasslands (“campos de altitude”) and usually located at middle elevations (1300-1400 m). Its flora is rich in epiphytes including shrubs that form a dense herbaceous cover; 3) “campos de altitude” – this vegetation occurs in altitudes above 1600m covering an area of 30km², mostly the mountaintops of the mountain range; due to its altitudinal

restriction, the “campos de altitude” are relatively isolated, bearing high levels of plant endemism (SAFFORD, 2007).

Three sampling sites were chosen as areas for fieldwork carried out from 1996 to 2004: Fazenda da Neblina (20°43'S, 42°29'W), Fazenda Brigadeiro (20°36'S, 42°24'W), and Serra das Cabeças (20°41'S, 42°28'W) (Fig.1). The first trapping seasons occurred between the years 1996 and 1998, just after the implementation of the state park, as part of a large vertebrate inventory project by the Museu de Zoologia João Moojen, Universidade Federal de Viçosa (PEREIRA *et al.*, 1998). The 1996-1998 trapping program focused only on the Fazenda da Neblina and the trapping effort was directed to the 1400m altitudinal interval. The second period of sampling took place four years later, between the years 2002 and 2004, and covered two additional sites, the Serra das Cabeças and the Fazenda Brigadeiro. The 53 days of total trapping summed a sampling effort of 4623 trap-nights (Tab.1).

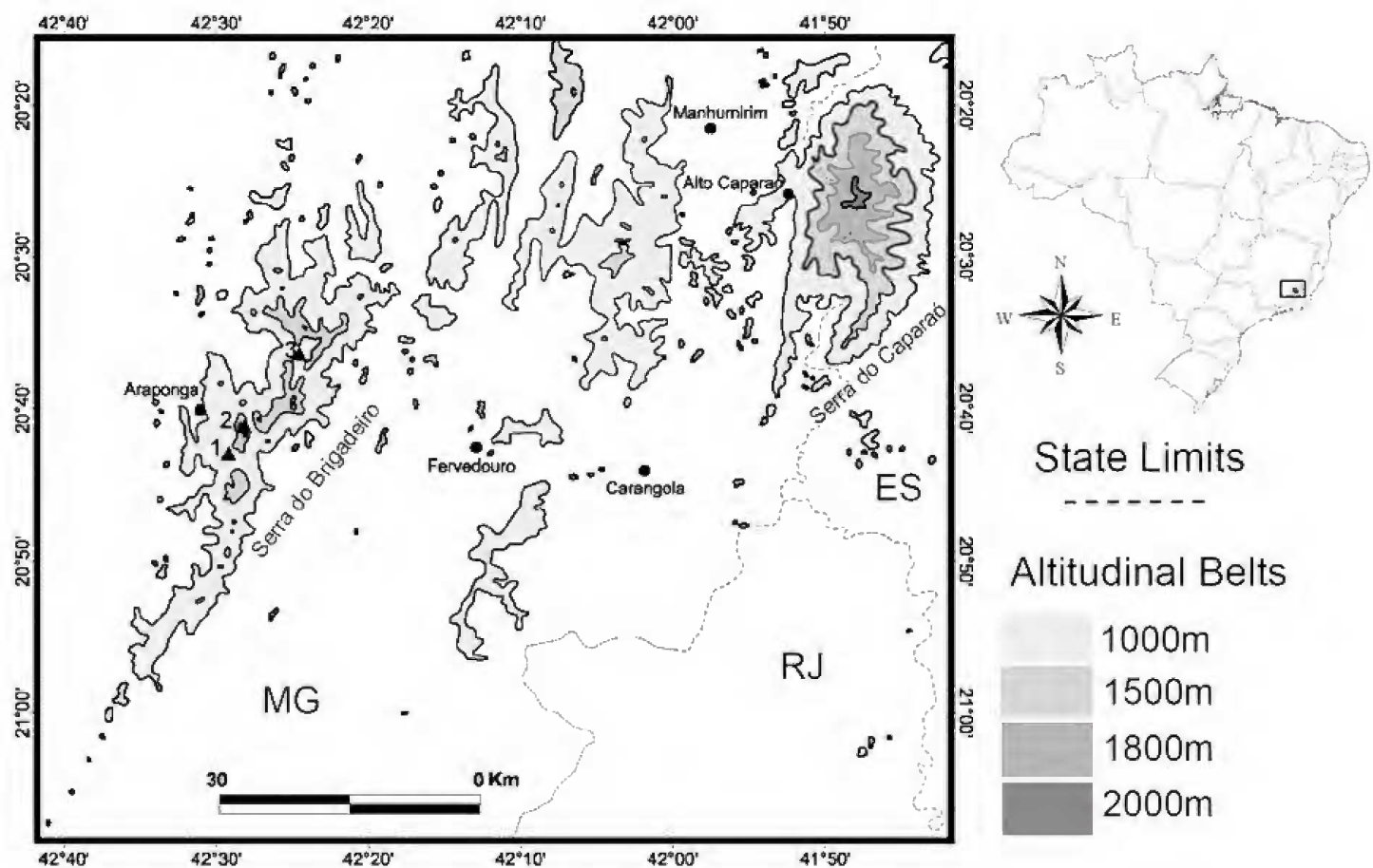


Fig.1- Location of study area in Minas Gerais State (southeastern Brazil) and physiography of the Serra do Brigadeiro mountain range and vicinities. (BA) Bahia State; (ES) Espírito Santo State; (MG) Minas Gerais State; (RJ) Rio de Janeiro State; (SP) São Paulo State. Sampling sites: (1) Fazenda da Neblina; (2) Serra das Cabeças; (3) Fazenda Brigadeiro.

TABLE 1. Trapping effort employed to sample the small mammal community in each altitudinal zone during inventories in the Serra do Brigadeiro State Park between 1996 and 2004.

ALTITUDINAL ZONE	SAMPLING EFFORT (TRAP-NIGHTS)	VEGETATIONAL TYPE	SAMPLING SITE
1200m (1200-1299m)	264	SubMontane Forest	Fazenda Brigadeiro
1300m (1300-1399m)	653	SubMontane Forest	Fazenda Neblina / Fazenda Brigadeiro
1400m (1400-1499m)	3168	SubMontane Forest / Transitional Areas	Fazenda Neblina / Fazenda Brigadeiro
1500 (1500-1599m)	163	Campos de Altitude	Fazenda Brigadeiro
1600 (1600-1699m)	204	Campos de Altitude	Fazenda Neblina
1800 (1700-1850m)	171	Campos de Altitude	Serra das Cabeças

The sampling site and the predominant vegetational type of each altitudinal belt are also showed.

SAMPLING METHODS

We used Sherman (9x9x23 and 9x9x31cm) and Tomahawk (15x15x31cm) live traps baited with banana, sardines, and maize flour to sample the local fauna of small rodents and marsupials. Traps were set mostly on the ground near tree roots, fallen logs, but occasionally some trapping stations were also set above the ground tied to lianas, bamboos, and tree trunks whenever possible. Trap lines were implemented as linear transects crossing distinct altitudinal zones (altitudes varying from 1200 to 1850m) in an attempt to sample the maximum altitudinal interval. Six elevation zones were established based on the altimetric interval covered by trapping lines (Tab.1).

Data on sex, measurements, habitat of capture, reproductive condition, and parasites were recorded for all individuals trapped. Specimens were prepared as standard vouchers and deposited at the collection of the Museu de Zoologia João Moojen, Universidade Federal de Viçosa (MZUFV; voucher numbers are listed in the Appendix), ensuring precise estimates of species diversity and a permanent documentation of the biological evidence (VOSS & EMMONS, 1996). Identification at the species level was guided by morphological comparisons with samples and published descriptions of confidently identified series from other localities deposited in Brazilian institutions. We followed the species diagnoses and

morphological definitions proposed by the most recent revisions in the case of taxonomically complex genera such as *Akodon* (GONÇALVES *et al.*, 2007), *Oligoryzomys* (WEKSLER & BONVICINO, 2005), *Oxymycterus* (GONÇALVES & OLIVEIRA, 2004), and *Gracilinanus* (COSTA *et al.* 2003; VOSS & JANSÁ, 2005).

CYTOGENETIC ANALYSES

Some species of rodents were cytogenetically analyzed in order to confirm taxonomic identifications and document the karyotypic diversity of the local small mammal populations. Mitotic metaphase chromosomes were obtained from specimens previously injected with 0.1% colchicine solution in the proportion of 1ml for each 100g. Bone marrow cells were extracted and treated in KCl 0.075M solution for 30min., being finally fixed and stored in Carnoy solution (3:1 Methanol/Acetic acid) (PATTON, 1967). Metaphases were visualized under conventional Giemsa staining and the karyotypes were determined by the diploid number (2n) and the number of autosomal chromosome arms (fundamental number - FN). At least 20 metaphases were analyzed for each species in order to obtain precise diploid and fundamental numbers. The best metaphases were photographed under an Olympus BX 60 Binocular Microscope attached to an image capturing system. The homologous chromosomes were grouped and arranged according to size and position of centromere, following LEVAN *et al.* (1964).

ECOLOGICAL ANALYSES

Species diversity is here termed as the number of species or species richness of a given area. Abundance estimates were calculated for each species as the proportion of individuals of a given species trapped in relation to the total of individuals sampled. The abundances were calculated at the local (each altitudinal zone) and regional (the whole study area) spatial scales. In the first case, only individuals trapped at the same altitudinal zone were counted in the abundance estimation. Trapping success (the number of individuals trapped in relation to sampling effort) was also measured at varying spatial scales and was interpreted as an estimate of the relative density of species. The altitudinal zones or habitats with highest trapping success for a given species likely represent sites where this species reaches its highest density. Statistical significance of differences in species richness, number of individuals trapped, and trapping success among the altitudinal zones was assessed by a *G*-test. Pairwise correlations between these parameters and altitude were assessed by Pearson product-moment correlation coefficients.

The completeness of the species richness estimated from the overall data was evaluated in two ways. First, we examined the topology of species cumulative curves in relation to sampling effort. The sampling units adopted for the construction of cumulative curves were the individual captures recorded (Hortal *et al.*, 2006). The temporal entries of species register were randomized (rarefaction) to produce standardized curves. Complete and more accurate inventories are expected to show asymptotic curves of species accumulation throughout fieldwork. A second approach was to extrapolate the species richness using the first-order jackknife nonparametric diversity estimator providing expected numbers of species, against which the observed richness was compared (Colwell & Coddington, 1994). These expected values of species richness correspond to the maximum number of species amenable to be sampled by our trapping methodology. The comparison between observed and expected richness provided a test of whether the observed diversity was biased by the unequal sampling effort in each altitudinal zone. All the calculations of cumulative functions were computed using the software EstimateS (Version 7.5, R. K. Colwell, <http://purl.oclc.org/estimates>). Statistically significant differences of inventory

performance along the altitudinal zones were evaluated by a *G*-test.

RESULTS

TAXONOMIC AND CYTOGENETIC DIVERSITY

Twenty-one non-volant mammal species from two orders and three families were recorded during the field surveys at the three sampling sites. Rodents comprised the most diverse assemblage, being represented by 14 species of the family Cricetidae and one species of the family Echimyidae (Tab.2). Marsupials of the family Didelphidae were represented by six species.

The cricetid genera recorded belong to the subfamily Sigmodontinae, and there is a considerable suprageneric diversity among them, as four tribes are represented. Most cricetid species are representatives of the tribes Akodontini and Oryzomyini, including *Thaptomys* and *Sooretamys*, two Atlantic forest endemic taxa (Musser & Carleton, 2005; Weksler *et al.*, 2006). Other endemic lineages are the thomomysines *Delomys* and *Juliomys*, which also have their distributions restricted to the Atlantic forest of southeastern and southern Brazil. Although most genera recorded are diverse in South America, many of them are monotypically represented in the study area. Important exceptions are the genera *Akodon*, *Oligoryzomys*, *Marmosops*, and *Monodelphis*, always represented by two sympatric species.

Cytogenetic analyses encompassed seven species of rodents and proved useful for the identification of populations of the Serra do Brigadeiro. *Oligoryzomys nigripes* presented $2n=62$, $FN=82$ based on two individuals analyzed, all formed by 11 pairs of submetacentrics and metacentrics chromosomes and 19 pairs of acrocentrics, a large submetacentric X and a small submetacentric Y (Fig.2A). The only male of *Oxymycterus dasytrichus* analyzed showed a karyotype with $2n=54$, $FN=62$, formed by a pair of large submetacentrics, 4 pairs of small metacentrics, 2 pairs of subtelocentrics (a large pair and a small pair), 19 pairs of acrocentrics of decreasing size (Fig.2B). *Thaptomys nigrita* displayed $2n=52$ and $FN=52$ based on 5 individuals analyzed, the chromosomal complement constituted of 24 pairs of acrocentrics, one pair of submetacentrics, a medium acrocentric X and a medium subtelocentric Y (Fig.2C). The 13 individuals of *Akodon cursor* analyzed displayed a

karyotype of $2n=14$ and $FN=18$, composed of three pairs of metacentric chromosomes, three pairs of acrocentrics, a small acrocentric X chromosome and a diminutive acrocentric Y (Fig.2D). The 10 karyotyped specimens of *Akodon serrensis* presented $2n=46$, $FN=46$, formed by one metacentric pair, 21 acrocentric pairs, a small acrocentric X and minute acrocentric Y (Fig.2E). The only karyotyped individual of *Cerradomys subflavus* showed $2n=54$, $FN=64$, presenting 6 pairs of submetacentrics and metacentrics, 20 pairs of acrocentric chromosomes, a medium acrocentric X and a medium metacentric Y (Fig.2F). Finally, the sole male of *Necomys lasiurus* analyzed showed $2n=34$, $FN=34$, formed by one pair of diminutive metacentrics, 15 pairs of acrocentrics with progressively decreasing sizes, a small acrocentric X and a small submetacentric Y (Fig.2G).

ABUNDANCE AND ALTITUDINAL DISTRIBUTIONS OF SPECIES

The most frequent species in the study area were the akodontines *Akodon cursor* (23.63%), *A. serrensis* (19.22%), and *Thaptomys nigrita* (17.4%). These species were dominant in all trapping periods, being captured in all habitats sampled. A diverse group of species presented intermediate abundances throughout the field studies with frequencies ranging from 1.5% to 6% of the total captures (Fig.3). This was the case of the cricetid rodents *Delomys sublineatus*, *Oligoryzomys nigripes*, *Sooretamys angouya*, *Oxymycterus dasytrichus*, and the didelphid marsupials *Gracilinanus agilis*, *Marmosops incanus*, *Monodelphis americana*, and *Philander frenatus*. This group also included species with more marked habitat preferences, most of them being trapped exclusively in forested habitats (submontane forests and transitional areas). A larger array of species was unevenly recorded during our studies, being represented by less than four individuals. These rare species were the marsupials *Marmosops paulensis*, *Monodelphis scalops*, the echimyid *Trinomys graciosus* and the cricetids *Calomys tener*, *Cerradomys subflavus*, *Necomys lasiurus*, *Nectomys squamipes*, *Oligoryzomys flavescens*, *Rhipidomys mastacalis* and the recently described *Juliomys ossitenuis*. All rare species were trapped in forests with the sole exception of *Necomys lasiurus*, recorded in an isolated rocky outcrop bordered by submontane forest.

In general, the most abundant species were also the more widespread across the altitudinal interval considered. *Akodon cursor*, *A. serrensis*, and *T.*

nigrita were trapped in at least five of the six altimetric bands and occupied the entire sampled altitudinal interval. The dominance pattern of each one of these species, however, varied considerably along altitudes. *Thaptomys nigrita* and *Akodon cursor* were the commonest small mammals at lower elevations (1200-1400m), but *A. serrensis* becomes more frequent than these species from mid to high elevations (1450-1800m). *Akodon cursor* is remarkably rare at high elevations (1800m), being represented solely by one individual out of 41 specimens trapped. The group of moderately abundant species also showed a few widespread species that occupied the entire altitudinal interval, such as *Oxymycterus dasytrichus* and *Monodelphis americana*. The majority of the rodent and marsupial species were much more restricted elevationally, with altitudinal limits rarely exceeding 1400m.

ALTITUDINAL VARIATION IN SPECIES RICHNESS AND TRAPPING SUCCESS

The diversity of non-volant small mammals in the Serra do Brigadeiro State Park varied significantly along altitudinal zones ($G=17.47$, $p=0.003$). The lowest and the highest altitudinal belts presented less species than the intermediate zones. Consequently, the species richness peaked at the middle of the altitudinal interval sampled, represented by the cote of 1400m, which harbors a richness of 18 species (Fig.4). The 1400m zone was also the most intensively sampled and a high correlation between species richness and number of individuals sampled ($r=0.90$, $p=0.001$) is readily apparent (Fig.4). Trapping success also varied considerably along the altitudinal gradient ($G=72.97$, $p<0.001$), but has no significant correlation with either species richness ($r=-0.43$, $p=0.531$) or altitude ($r=0.63$, $p=0.177$). The high altitudinal belts of 1500 and 1800m were the most successful in captures (14-24%, Fig.4), but were also more depleted in species number (3-5 species). Conversely, the lower altitudinal belts dominated by forested habitats showed relatively low capture rates (8.6-7.4%), but were more species rich than the higher zones (7-18 species).

COMPLETENESS OF THE INVENTORY AND ESTIMATED DIVERSITY

A species accumulation curve was constructed following the observed sequence of species records throughout the inventory (Fig.5a). The first two years of inventory (1996-1997) were characterized by a steep increase in the number of species listed.

TABLE 2. List of species captured across six altitudinal zones in the Serra do Brigadeiro State Park, Minas Gerais.

TAXA	KARYOTYPE		ELEVATION (m)						TOTAL
	2n	FN	1200	1300	1400	1500	1600	1800	
Order Didelphimorphia									
Family Didelphidae									
<i>Gracilinanus agilis</i>	-	-			7				7
<i>Marmosops incanus</i>	-	-	1	6	13				20
<i>Marmosops paulensis</i>	-	-			3				3
<i>Monodelphis americana</i>	-	-		1	5			1	7
<i>Monodelphis scalops</i>	-	-			1				1
<i>Philander frenatus</i>	-	-		3	7				10
Order Rodentia									
Family Cricetidae									
Subfamily Sigmodontinae									
Tribe Akodontini									
<i>Akodon cursor</i>	14	18	5	18	61	1	4	1	90
<i>Akodon serrensis</i>	46	46	3	3	31	15	2	20	74
<i>Necomys lasiurus</i>	34	34		2					2
<i>Oxymycterus dasytrichus</i>	54	64	1	3	15	1	3	9	32
<i>Thaptomys nigrita</i>	52	52	7	14	36			10	67
Tribe Oryzomyini									
<i>Cerradomys subflavus</i>	54	64			1				1
<i>Oligoryzomys flavescens</i>	-	-			1				1
<i>Oligoryzomys nigripes</i>	62	82		2	16	6			24
<i>Nectomys squamipes</i>	-	-			2				2
<i>Sooretamys angouya</i>	-	-	3	1	6				10
Tribe Phyllotini									
<i>Calomys tener</i>	-	-			1				1
Tribe Thomasomyini									
<i>Delomys sublineatus</i>	-	-	1		22				23
<i>Juliomys ossitenuis</i>	-	-			4				4
<i>Rhipidomys mastacalis</i>	-	-			3				3
Familiy Echimyidae									
Subfamily Eumysopinae									
<i>Trinomys graciosus</i>	-	-		2					2
TOTAL			21	55	235	23	9	41	384

The karyotypes of seven selected cricetid rodents and the number of individuals recorded per altitudinal zone for all species are showed.

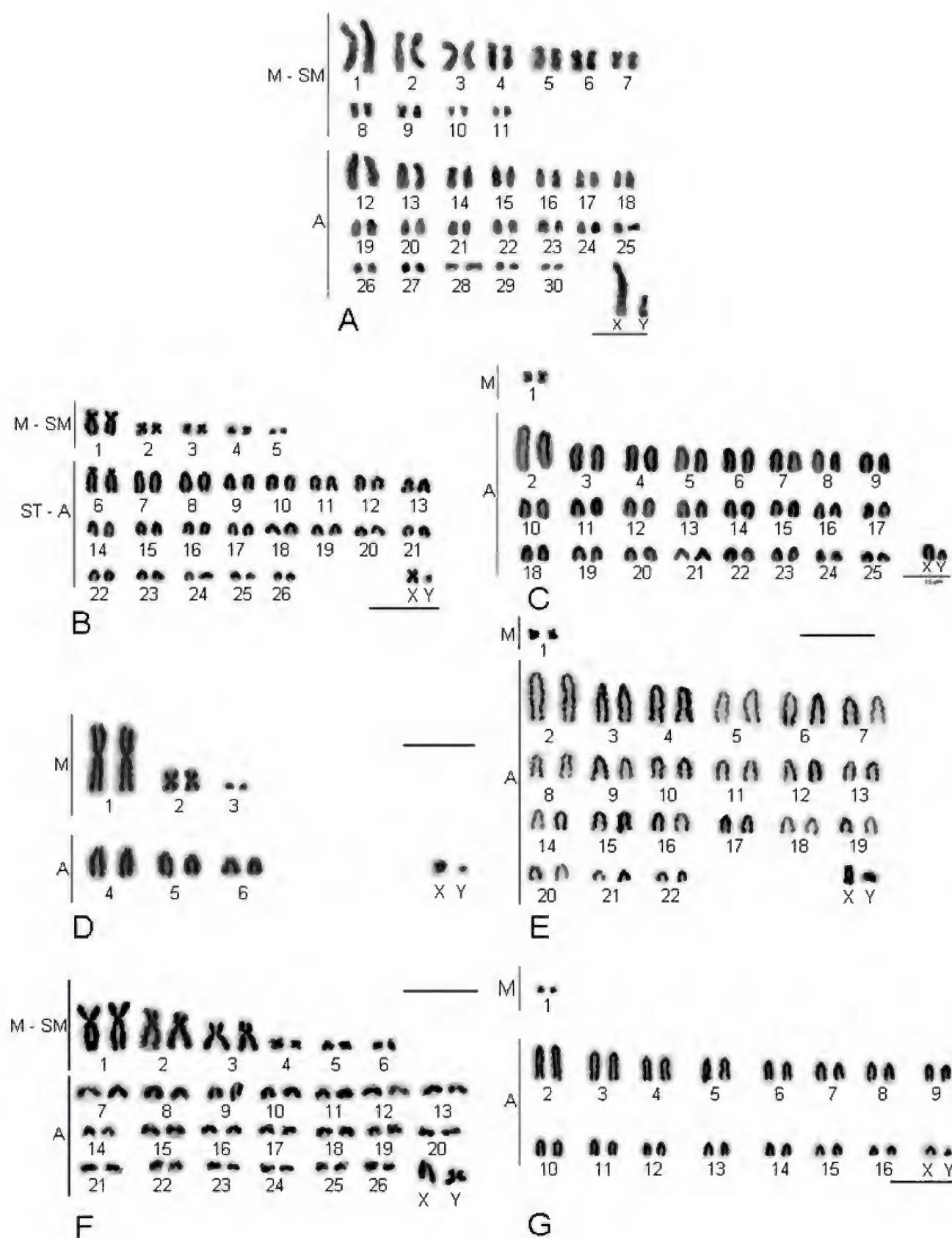


Fig.2- Conventional Giemsa staining of chromosomes of selected species of cricetid rodents from Serra do Brigadeiro: (A) *Oligoryzomys nigripes*; (B) *Oxymycterus dasytrichus*; (C) *Thaptomys nigrita*; (D) *Akodon cursor*; (E) *Akodon serrensis*; (F) *Cerradomys subflavus*; (G) *Necromys lasiurus*. Scale = 10µm. Abbreviations: (M) metacentric, (SM) submetacentric, (A) acrocentric, (ST) subtelocentric.

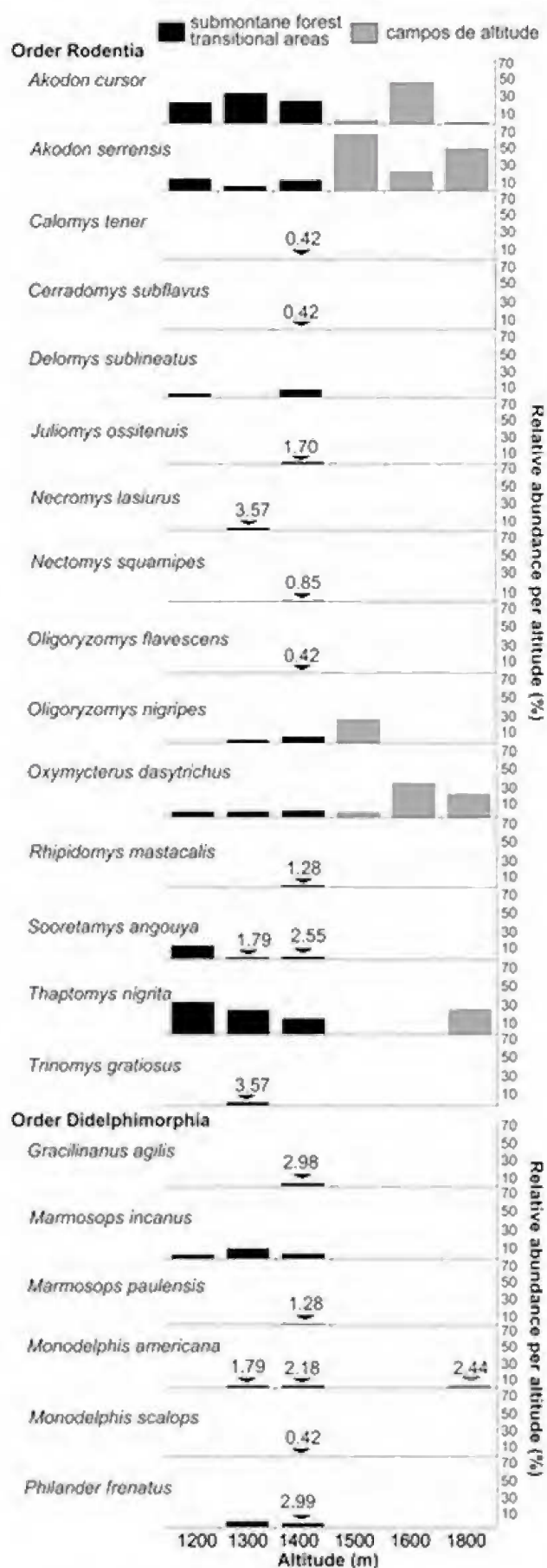


Fig.3- Altitudinal variation in relative abundance of small mammal species recorded in the Serra do Brigadeiro State Park, Minas Gerais.

After two short trapping seasons without any additions, more intensive sampling (160 individuals trapped) carried out during 2003 added three more species at the last captures. The final year of inventory added only one more species to the list, which stabilized at 21 species around the last 120 individuals trapped.

The temporal order of species records was randomized to generate a standardized curve for the complete inventory, in order to evaluate whether the species curve showed a stabilized plateau. As shown in figure 5b, the standardized accumulation curve does not show a plateau or an asymptote. The Jackknife 1 estimator indicates an expected diversity of 26 species in the area, suggesting that the trapping methods sampled roughly 80% (21 species) of the actual diversity.

To check the inventory performance along the altitudinal zones, standardized cumulative curves were also obtained for each of six altitudinal bands defined (Fig.5C-H). The cumulative curves of species sampled per altitude did not show an asymptotic behavior in any altitudinal zone sampled, indicating that additional sampling effort is needed to reach a stabilized number of species. When compared to the estimates provided by Jackknife, the altitudinal inventories were 82% complete in average. The 1300m zone inventory (Fig.5D) approached the expected richness more closely (92% of the expected richness) while the 1600m survey (Fig.5G) was the less completely inventoried (75% of the expected value). These variations in completeness, however, are not statistically significant ($G=1.07$, $p=0.96$) and the inventory performance along the six altitudinal zones can be considered as equal.

There was no correlation between the sample sizes (number of individuals trapped) and completeness ($r=0.19$, $p=0.85$), as the richest and most exhaustively sampled altitudinal zones were not necessarily the more completely inventoried (e.g., 1400m zone, Fig.5D). Nevertheless, the expected richness followed the same altitudinal pattern of the observed richness, with the highest diversity peaking at middle elevations.

DISCUSSION

SPECIES COMPOSITION IN THE SERRA DO BRIGADEIRO AND CYTOGENETIC CONSIDERATIONS

Faunal inventories are a key priority for the conservation of the mammalian diversity in the

Atlantic forest. When documented by voucher specimens, mammal inventories greatly contribute to assess the taxonomic diversity of poorly known mammalian groups by providing the raw material used for systematic revisions (PATTERSON, 2002). This is the case of most marsupial and rodent genera in the Neotropical region, groups for which new species are continuously being described from samples of eastern Brazil, especially from remnants of Atlantic forest.

The present study contributed to fill the gap about the small mammals of the Serra do Brigadeiro listing 21 species of marsupials and rodents. The previous effort to preliminarily sample the diversity of the park made by COSTA *et al.* (1994) listed 10 species, most of which were recorded in this study, except for the common black-eared opossum, *Didelphis aurita*. Including this record, the total number of non-volant small mammal species in the Serra do Brigadeiro increases to 22. This richness is as high as those of other Atlantic forest sites in southeastern Brazil, which generally present between 21-24 species. The Mata do Paraíso forest reserve (670m), in Viçosa Municipality, and the Rio Doce State Park (230-515m), Marliéria, both in the State of Minas Gerais and relatively near from Serra do Brigadeiro, showed similar diversities of 21 and 24 species, respectively (LESSA *et al.*, 1999; FONSECA & KIERULFF, 1989). The Caparaó National Park, a major montane area also near the study site, presented 22 species (BONVICINO *et al.*, 1997; COSTA *et al.*, 2007). The Santa Lúcia Biological Station (550-950m), in the Espírito Santo State, showed 21 species (PASSAMANI *et al.*, 2000) and the Morro Grande Forest Reserve (860-1070m), in São Paulo State, displayed 23 species (PARDINI & UMETSU, 2006). The only Atlantic forest area with a strikingly rich small mammal assemblage is the Itatiaia National Park, located on a major massif (900-2700m) in the southern Mantiqueira complex, which showed a diversity of 33 species of small mammals (didelphid marsupials, cricetid, and echimyid rodents) (GEISE *et al.*, 2004).

Some species of marsupials and rodents found in the Serra do Brigadeiro are representatives of a typical Atlantic forest fauna, as they have their distributions circumscribed to the limits of this domain. Among these forest dwelling mammals are *Akodon serrensis*, *Delomys*

sublineatus, *Juliomys ossitenuis*, *Marmosops paulensis*, *Monodelphis scalops*, *Oxymycterus dasytrichus*, *Philander frenatus*, *Sooretamys angouya*, *Thaptomys nigrita*, and *Trinomys graciosus*. With the exception of *Philander frenatus*, *Sooretamys angouya*, and *Thaptomys nigrita*, these forest taxa also represent a geographically more restricted group of endemics, as their distributions rarely extend further north to the northeastern part of the Atlantic forest. *Marmosops paulensis* and *Juliomys ossitenuis*, for example, are found only in submontane and montane forests of southeastern and southern Brazil (MUSTRANGI & PATTON, 1997; COSTA *et al.*, 2007). The remaining species found in the study area comprise more widespread taxa, distributed throughout more than one morphoclimatic domain in South America, such as *Akodon cursor*, *Calomys tener*, *Cerradomys subflavus*, *Gracilinanus agilis*, *Oligoryzomys nigripes*, *Marmosops incanus*, *Monodelphis americana*, *Necomys lasiurus*, and *Nectomys squamipes*.

The cytogenetics served as an additional tool in the diversity estimates, complementing taxonomic identifications already advanced by morphological comparisons in several cases. All karyotypes recovered from our samples were similar to those already published for other populations of the same taxa in Atlantic forest confirming their presence in the Serra do Brigadeiro. Especially in the case of the genus *Akodon*, cytogenetic analyses confirmed the presence of *Akodon cursor* characterized by the karyotype $2n=14$, $FN=18$, and of *Akodon serrensis* characterized by $2n=46$, $FN=46$ (Fig.2).

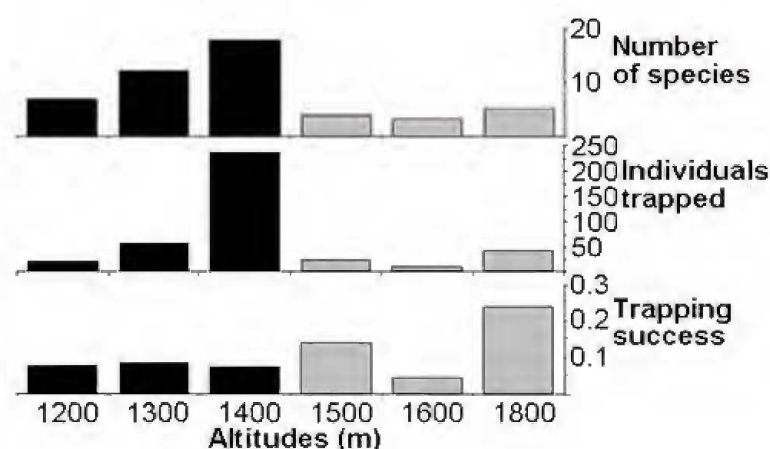


Fig.4- Altitudinal variation in species richness, number of individuals trapped, and trapping success in Serra do Brigadeiro State Park, Minas Gerais.

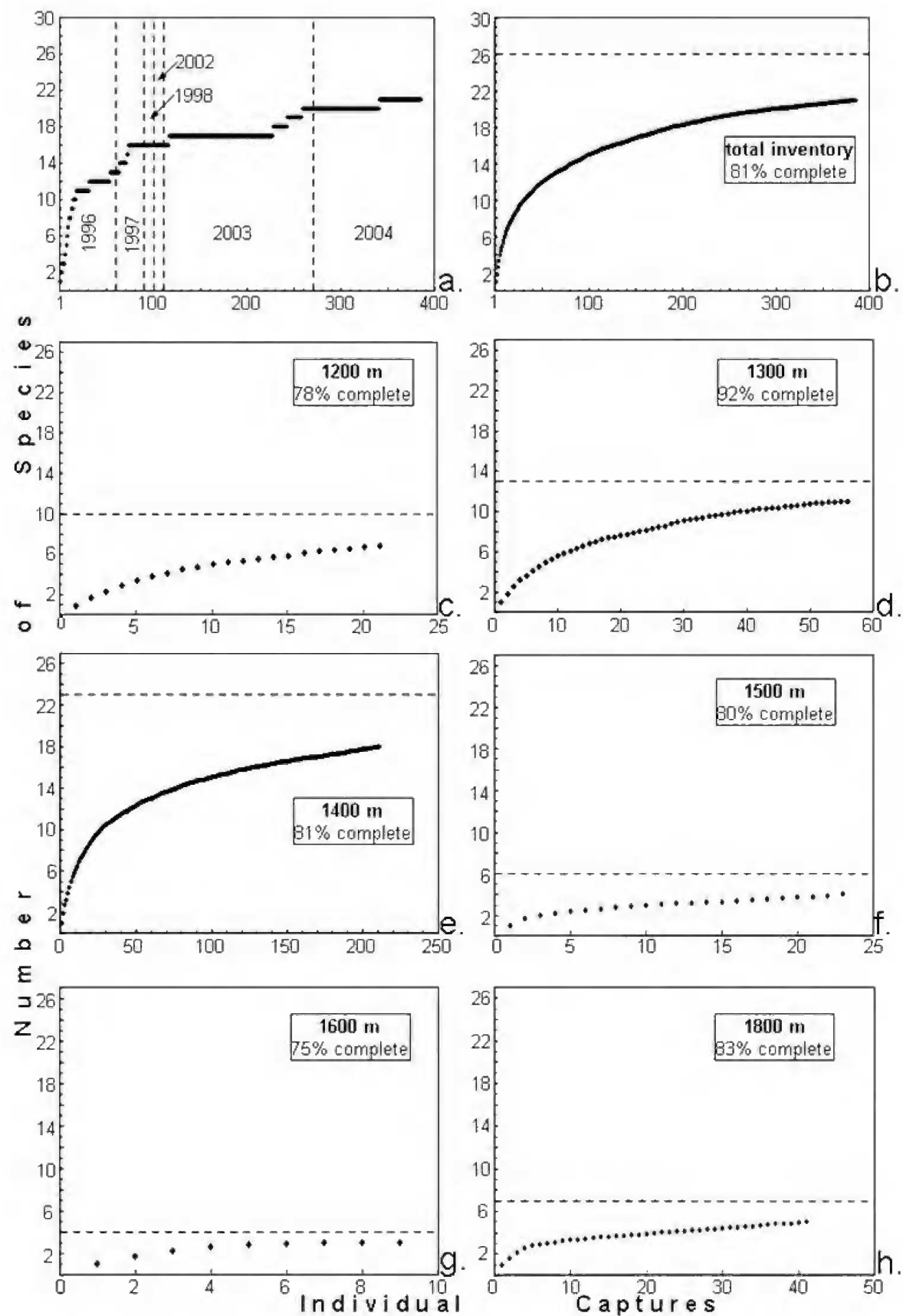


Fig.5- Non-volant small mammal species accumulation curves, expected numbers of species (horizontal dotted lines – Jackknife 1), and relative performance of the inventory in the Serra do Brigadeiro State Park, Minas Gerais: (A) non-standardized and (B) standardized accumulation curves for the entire inventory; (C-H) standardized curves and inventory performance for the 1200m, 1300m, 1400m, 1500m, 1600m, and 1800m altitudinal zones.

Species of this genus in eastern Brazil are difficult to identify due to the high morphological similarity and karyological characters have been an important criterion for species recognition in the group (FAGUNDES *et al.*, 1998; CHRISTOFF *et al.*, 2000). A high degree of cytogenetic polymorphism has been reported for *A. cursor* populations in Southeastern Brazil ($2n=14$, 15 and $FN=18-21$), but remarkably only the $2n=14$, $FN=18$ was found among karyotyped specimens from Serra do Brigadeiro. Other identifications complemented by karyotypic data were the presence of *Oligoryzomys nigripes*, with $2n=62$, $FN=82$ (WEKSLER & BONVICINO, 2005) and *Cerradomys subflavus* with $2n=54$, $FN=64$ (BONVICINO, 2003).

The taxonomic and biogeographic knowledge of many taxa found in the Serra do Brigadeiro has been improved by recent taxonomic revisions. This is the case for *Marmosops paulensis* (MUSTRANGI & PATTON, 1997), *Philander frenatus* (PATTON & SILVA, 1997), *Oxymycterus dasytrichus* (GONÇALVES & OLIVEIRA, 2004), *Cerradomys subflavus* (BONVICINO, 2003; WEKSLER *et al.*, 2006), and *Sooretamys angouya* (WEKSLER *et al.*, 2006). Remarkably, one species of arboreal cricetid recorded at Serra do Brigadeiro, *Juliomys ossitenuis*, has only recently been described (COSTA *et al.*, 2007), suggesting that the fauna of the area is by no means exhaustively studied. This is also suggested by the cumulative species curve and expected richness estimates, which show that at least five species of small mammals are likely missing from the observed list (Fig.5B) and may be recorded with additional sampling effort. The lack of arboreal echimyids (*e.g.*, *Kannabateomys amblyonyx* and *Phyllomys pattoni*) as well as relatively common marsupials (*Caluromys philander* and *Metachirus nudicaudatus*), for example, indicates that additional trapping in the forest canopy may be promising in revealing new records. Sampling by pitfall traps have allowed to record species rarely caught in live traps (*e.g.*, *Bibimys labiosus*, *Blarinomys breviceps*, *Euryzygomatomys spinosus*, and *Rhagomys rufescens*) and should also be implemented in future studies.

ALTITUDINAL VARIATION IN SPECIES COMPOSITION, RICHNESS, AND ABUNDANCE

Recent work on the effects of altitude in the diversity of non-volant small mammals has shown that the maximum species richness is usually found at middle elevations (MCCAIN, 2004; SANCHEZ-CORDERO, 2001). This recurrent pattern has been termed the

Mid-Domain model, in which species ranges of variable sizes are predicted to overlap more intensively at the center of a hard bounded area, resulting in a highest accumulation of species at the mid-point (COLWELL *et al.*, 2004). This prediction has been used as a null hypothesis and any deviations from the mid-domain model have been interpreted as cases where ecological and historical processes may have shaped or constrained the distributions of species and species richness.

In the Serra do Brigadeiro the upper and lower altitudinal zones are less diverse than the intermediate belt (1400m). At a first glance, this pattern is suggestive of a mid-domain effect, but methodological factors have to be taken into account. The highest expected and observed richness peak is located at the most intensively sampled altitudinal zone, leading to a high correlation between species richness and number of individuals captured. Thus, the observed pattern could likely represent a sampling artifact, in which the observed species richness was strongly biased by the sampling effort (LOMOLINO, 2001). On the other hand the comparisons of inventory performance across altitudes (Figs.5C-H) show that the six altitudinal zones were equally well surveyed, adding some support to the mid-domain pattern. Only continued trapping efforts in the upper and lower elevations could allow a test between the Mid-Domain effect and a sampling artifact hypothesis.

Another idea frequently evoked to discuss mid-domain patterns is the community overlap or ecotone hypothesis, in which peaks of species richness are expected to be found where adjacent communities overlap (MCCAIN, 2004). The majority of the rodent and marsupial species restricted to middle elevations presents scansorial or arboreal habits and is closely associated to the forest habitat. Nevertheless, terrestrial and more habitat-generalist species such as *Akodon serrensis*, *Oxymycterus dasytrichus*, and *Thaptomys nigrita* occupied the entire altitudinal interval sampled, overlapping much of their altitudinal distributions with forest taxa in the lower altitudes and extending their ranges up to the highest mountaintops surveyed. Since there are no species exclusively found at the highest altitudinal zones, there is no evidence that more than one community of marsupials and rodents is present at the Serra do Brigadeiro. This pattern suggests that the concentration of species in the 1300-1400m zones could rather be an effect of species-specific ecological limits than a result of community overlap or transition, as also noted by MCCAIN (2004) studying small mammals in a montane area of Costa Rica.

In addition to species richness and composition, the overall trapping success varied significantly across altitudinal zones. Assuming that the methodology (traps, bait) was the same for the entire altitudinal interval, the variation in trapping efficiency can be interpreted as a response to local abundance of small mammal species (KIKKAWA, 1964). All altitudinally widespread taxa increase their abundances at the highest altitudinal zones with the sole exception of *A. cursor*, which is extremely rare at 1800m. A pattern of ecological and altitudinal segregation among *Akodon* species has been reported by GEISE *et al.* (2005), involving *A. cursor* and *A. montensis*. The results found here extend this pattern to *A. serrensis*, a species that in the Serra do Brigadeiro virtually substitutes *A. cursor* at elevations higher than 1600m. The overall increase in density presented by widespread species is apparently not related to species richness, since similarly diverse elevational zones differ remarkably in trapping success (*e.g.*, 1800m versus 1200m). The area available seems to be a putative causal factor that in combination with the reduction in species number could lead to an increased density of few species in the reduced area available at mountaintops.

Major assessments and additional trapping in mountainous regions in southeastern Brazil are necessary to elucidate the mechanisms related to the effects of altitude in small mammal communities. Altogether, additional sampling in the upper and lower elevational bands of Serra do Brigadeiro would be needed to consistently test for hypotheses about the influence of altitude in species richness.

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APPENDIX

Specimens analyzed in this study and deposited in the Museu de Zoologia João Moojen, Universidade Federal de Viçosa (MZUFV).

Akodon cursor: MZUFV 512, 515, 516, 519, 521, 538, 548, 560, 570, 617–619, 679, 680, 1077, 1149, 1152, 1157–1171, 1173–1186, 1214–1221, 1226–1233, 1235, 1241, 1244–1246, 1250, 1253, 1263–1270, 1277, 1285, 1288, 1301, 1625, 1629, 1632, 1636, 1647, 1649, 1652, 1657.

Akodon serrensis: MZUFV 510, 520, 540, 541, 551, 555, 563, 564, 571, 709, 614–616, 1076, 1148, 1150, 1151, 1153–1156, 1172, 1213, 1218, 1231, 1234, 1242, 1243, 1248, 1249, 1251, 1252, 1254, 1266, 1267, 1278–1281, 1284, 1286, 1287, 1293–1300, 1626–1628, 1630, 1631, 1633–1646, 1648, 1650, 1651, 1653–1656.

Calomys tener: MZUFV 514.

Cerradomys subflavus: MZUFV 1132

Delomys sublineatus: MZUFV 509, 511, 518, 536, 542, 544, 553, 554, 556, 623, 678, 1137–1140, 1205, 1236, 1615–1617.

Gracilinanus agilis: MZUFV 534, 539, 545, 559, 565, 711.

Juliomys ossitenuis: MZUFV 552, 573, 608, 627, 679, 683.

Marmosops incanus: MZUFV 624, 626, 1099–1105, 1125, 1126, 1207, 1237, 1283, 1304, 1604–1607, 1611.

Marmosops paulensis: MZUFV 1608–1610.

Monodelphis americana: MZUFV 547, 1106, 1194, 1206, 1282, 1601–1602.

Monodelphis scalops: MZUFV 1592.

Necomys lasiurus: MZUFV 1107, 1108.

Nectomys squamipes: MZUFV 637, 677.

Oligoryzomys flavescens: MZUFV 606.

Oligoryzomys nigripes: MZUFV 513, 517, 535, 537, 546, 549, 557, 558, 562, 625, 1136, 1141, 1142, 1618–1624.

Oxymycterus dasytrichus: MZUFV 569, 621, 628–631, 639, 1119–1122, 1133, 1134, 1198–1204, 1238, 1256–1259, 1289, 1290–1292, 1612–1614.

Philander frenatus: MZUFV 529, 530, 1098, 1135, 1305–1309.

Rhipidomys mastacalis: MZUFV 508, 632.

Sooretamys angouya: MZUFV 522, 1131, 1594–1600, 1603.

Thaptomys nigrita: MZUFV 533, 543, 561, 566–568, 572, 622, 1109–1118, 1123, 1127–1130, 1143–1147, 1189–1193, 1208–1212, 1222–1225, 1239, 1240, 1247, 1255, 1260–1262, 1270–1276, 1582–1591, 1839.

Trinomys graciosus: MZUFV 1124, 1593.